Early Journal Content on JSTOR, Free to Anyone in the World

This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at http://about.jstor.org/participate-jstor/individuals/early-journal-content.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact support@jstor.org.

THE GENETIC RELATIONSHIP OF PARASITES[1]

FRANK DUNN KERN

Parasitism is a mode of life having many forms and degrees. Nutritional dependence may be partial, temporary, or complete. All possible intergradations exist. It has been estimated that a large percentage of the total number of seed plants may use complex food derived from other organisms and yet only a comparatively few assume a mode of life which has been regarded as parasitic. Gradations also connect the organism, which is dependent upon other living organisms for nourishment, with those which are dependent upon organic, but non-living, food.

Organisms may be classified physiologically as parasites, saprophytes, and autophytes (or holophytes) but such a classification does not coincide with a taxonomic one. Upon morphological grounds parasites are variously distributed in the taxonomic series with independent or saprophytic forms. If our taxonomic classifications can be regarded as representing phylogenetic relationships their arrangements not only suggest the evolution of parasites from free-living ancestors but also indicate many separate points of origin. The presence of free stages in the life-cycle of many parasites; the frequent occurrence of temporary parasitism; and the close morphological resemblances between some independent and some dependent forms afford abundant evidence to justify such a view.

Organic dependence may have begun gradually or it is possible in some instances that the time element may not have been a factor and that parasitism may have come about as a sudden mutation. Plausible explanations of the origin of the parasitic habit in animals do not seem so difficult as in plants. There is the possibility that the seeking of shelter may have been the starting point for some animal forms, others may have found protection accidentally having been swallowed in an embryonic or even adult condition. It has been suggested that in many cases the habit may have begun "with the naturally more sluggish females, prompted not by hunger, but by the impulse to seek some conveniently sheltered place for the birth of the young." It may be possible eventually to gain some usable hints from the past ages but parasitic conditions are so dependent upon adaptations in the physiology and soft structures that the record in the rocks is exceedingly fragmentary and difficult to interpret.

---

[1] Invitation paper read at the symposium on "The Genetic Relationship of Organisms" before the Botanical Society of America at Philadelphia, December 30, 1914. Contributions from the Department of Botany, Pennsylvania State College, No. 3.

When parasitism is suggested the one feature concerning the parasite which presents itself most strongly is that of degeneration. The dogma of degeneration is so thoroughly drilled into the minds of the students of biology everywhere that parasitism and degeneration seem unalterably linked together. We are prepared for the expressions that parasites "are more or less degenerate according to the extent of their parasitism" or that parasitism "unfailingly involves degeneration." Although we may expect old and popular beliefs to be overthrown at any time there seems to be much in favor of the correctness of this one. So far as the seed plants are concerned there is evidence of somatic degeneration, consisting chiefly of reductions or atrophies of the shoot and root, even in those forms which are only partially parasitic; while those which are fixed parasites may be still further reduced, the root failing to develop, the shoot remaining unbranched, the leaves lacking chlorophyll and frequently appearing as colorless bracts. With regard to the spore plants it is not so easy to form judgments concerning possible somatic modifications since there are likely to be long genetic series of heterophytic forms and no clearly related autophytic groups to form a basis for comparison.

As regards sexuality it has been a widely accepted doctrine that the parasitic mode of life leads to its disappearance. Investigations by Ernst and Schmidt on the root parasite *Rafflesia* have caused them to draw the general theoretic conclusion that so far as seed plants are concerned parasitism does not tend to the disappearance of sexuality. Other studies have, however, shown that the fruits and seeds may show various specializations. In the case of the fungi we are not surprised to find in an authentic text-book, now only fifteen years old, the statement that sexual reproduction is common in the Phycomycetes, occasionally occurs in the Ascomycetes, and is not certainly known to exist in the Basidiomycetes, with the added explanation that probably certain of the higher forms of fungi that have lost their sexual methods of reproduction have been derived from the lower fungi. Recent researches have shown that the old belief in the disappearance of sexuality in the parasitic fungi is no longer tenable. Harper has summed up the situation for the fungi in the statement that "the evidence is now generally accepted that either a typical conjugation of normally differentiated gametes and their nuclei or some form of substitute for it is everywhere present." The very fact, however, that there is here interpolated the phrase "or some form of substitute for it" suggests strongly that although there may not be a disappearance of sexuality there may be a degeneration. In fact the author just quoted states further that the fungi exhibit some fundamental modifications of the process of sexual fusion as found elsewhere. The question whether these variations are to be regarded as degenerations may be debatable but inasmuch as they are considered substitutions for sexual fusions that would appear to be implied. It should be noted here that while sexual reproduction can be shown not to be entirely impossible for certain forms yet its occurrence may be exceedingly rare. Long patient researches with some forms such as the late blight fungus of potatoes have led to an almost inevitable conclusion that there is not a disappearance of sexuality but that there is a loss of sexual vigor. It seems reasonable to conclude that the presence of both somatic and sexual modifications in parasites warrant the continued association of degeneration with parasitism.

In connection with this view that parasitism is a degenerate adaptation it would be interesting to know whether there are any cases where the parasitic habit has been conquered and a return made to a normal independent existence. MacDougal in speaking of the higher plants says that it is usual to consider them "as passing down an inclined plane of atrophies, which would ultimately lead to their extinction, without reference to the abundance of development of the host forms." He has not in his investigations obtained the slightest hint which would indicate the possibility of a retracement by which a parasite might regain its standing as an independent. Nor is there any evidence from the bacteria or fungi to suggest that the parasitic habit when once established ever can be overcome. Some investigators hold the view that certain groups of obligate fungous parasites have made morphological advances of a sporophytic nature but this is questionable and even if true could not be taken as an indication of a possible step toward abandonment of parasitism. Some evidence which seems to point in this direction comes from the animal kingdom and is furnished by a paleontologist. The case referred to is that of the parasitism of the gastropods on the crinoids and has been very clearly set forth by Clarke. Gastropods of the limpet type were parasitic on crinoids from the Silurian on to the latter part of the Paleozoic when all traces of such a condition ceased. The evidence points toward the cessation of this parasitic condition during Carboniferous ages. Clarke believes "that all the positive and all the negative evidence we can now adduce on this deeply important subject favors the presumption that the habit was abandoned or at least, to speak in terms of simple casuistry, was lost." There are no parasitic snails on crinoids today, but close allies of the crinoids are parasitized by gastropods of the limpet type. This, however, is held to be entirely independent of the former association between these groups.

Much has been written concerning the nature and origination of parasitism but much remains for further experimentation before the factors involved can be understood. In order to form proper conceptions it is necessary not only to consider the parasite and its weapons, but also the host with its defense, so that the question of the origin and nature of parasites is inseparably associated with those phenomena generally grouped under the term immunity. We must take into account also the effects of the environment upon both parasite and host. The available evidence indicates such a difference in the genetic physiology of parasites belonging to the higher and lower plants, respectively, that it may be best to discuss the groups separately.

The parasitic seed plants form a series of isolated groups each of which bears a more or less evident genetic relationship to some independent group. Any theory of origination must take into account the undoubted existence of a number of disconnected points or levels oforigin. MacDougal has extensively investigated the conditions under which two plants may enter into the relation of host and parasite by growing one plant upon another and has concluded that "the ruling factor was in all cases the osmotic ratio between the sap of the two plants," a greater osmotic pressure being necessary in the incipient parasite. Of course many other factors are involved for one plant is not able to parasitize another simply because it possesses a higher osmotic pressure. It seems likely that parasites among the seed plants arose directly from independent ancestors without any intervening saprophytic condition such as probably existed in the evolution of the fungi. The first step intervening between independence and dependence in the seed plants may have been the absorption of water and food materials, the taking up of complex foods being a later development. This is in accord with a theory hazarded by Cowles who adds that as a final development there comes the loss by the seeds of the power to renew their growth, except when in contact with the host, and the development of a univorous habit.

As intimated in the foregoing paragraph there is evidence indicating that the parasitic lower plants (bacteria and fungi) have developed from independent plants not directly but through intermediate saprophytism. There are numerous transitional stages from autophytes to saprophytes and on to facultative parasites, ending finally in obligate parasitism. The development of the capacity to take in organic foods in a saprophytic manner seems to be a simpler first step for these forms, rather than the absorption of water and food materials in a parasitic way, and at the same time the existing forms grade into one another along such a probable course of development. Even after parasitism is attained there are still degrees of differentiation. The forms which can continue without sufficient detriment to the host to cause its death, and hence their own, are to be regarded as on a higher plane of development than those whose aggressive growth soon results in death for both host and parasite. Another condition which is agreed by many to indicate a high parasitic evolution is the physiological dependence upon a very restricted set of hosts. The greater the restriction, which may be a single host species, or even a variety, the higher the stage of parasitic development.

Concerning the independent forms which may be looked upon as most nearly representing the probable ancestors of such forms as the parasitic bacteria and fungi there is general agreement in a broad way but naturally differences of opinion upon many important points. The probable connection between some dependent and independent forms has received definite recognition in the classifications used by some taxonomists. Bessey no longer maintains the Phycomycetes co-ordinate with the groups of higher fungi but places them in the phylum with the tube algae upon morphological grounds. In like manner the Synchitriaceae are grouped with the unicellular green algae. The series classed as higher fungi are more isolated and retain standing as a separate phylum with debate still going on as to their relationships and interrelationships.

In a recent paper Jones has emphasized the fact that the fundamental problems of parasitism remain unsolved, that "we have scarcely begun the study of the intimate relations of parasite and host, the conditions and results of parasitism." He comments further that the very simplicity of the plant's organization makes these relations more difficult to investigate than with the animal, the cell being the unit, not the organism, the study of chemical interrelations is rendered highly difficult. "Such problems," he says, "call for the combined skill of pathologist, physiologist, cytologist, and chemist." These forces, however, have not been mobilized adequately as yet.

Chemotropism is frequently put forward as a factor involved in the origin of parasitism in the lower plants. Massee goes so far as to assert infection is due to positive chemotaxis. If it is the pulling power of some substance within a host which causes fungi to enter, it is difficult to explain highly restricted parasites. Either very few hosts contain the proper substance or all others must contain something to neutralize this attraction or something of a more powerful repellant nature. Neither view seems adequate to give us a conception of a large percentage of the world of plants with parasites more or less specialized to themselves. It must be kept in mind also that mere entrance of a fungus is only preliminary and not necessarily indicative of parasitism. The theories of immunity come to mind, pass in review, and leave us unsatisfied. One investigator states that "immunity depends chiefly (perhaps entirely) upon the ability of the cytoplasm of the host-cells to resist infection by secreting anti-toxins which will kill the mycelium of the fungus." Tannin, vegetable acids, and oxidizing enzymes have been named as possible toxic substances. Others would not place the burden of keeping invaders out upon the cell-contents of the host, but explain the failure of parasites to grow promiscuously upon their lack of development of cytolytic enzymes sufficient to break down the barrier offered by the cell wall. It makes little difference which of the theories has the most supporters or which one appears most plausible; not one of them, or any combination of them, gets at the real intimate relation which must exist between host and parasite. Chemical, food, or structural features, as far as we are able to appreciate them, seem unable to explain why one parasite can attack only one variety of a single host species while another similar parasite may attack all the varieties, other species of the genus, and perhaps even extend to other closely related genera.

Our problem would be sufficiently baffling if we were left to consider only the relation between a parasite and its host, or hosts when it passes to several allied forms, as indicated in the foregoing paragraph. No matter how difficult this may appear to be we are obliged to designate this as simple parasitism. To contrast with this there are the cases of parasites which are known to inhabit wholly different and unlike hosts in different stages of their life histories. Such a surprising and, as it seems, unnecessarily complex parasitism exists in both animal and vegetable kingdoms. In those species which change hosts, and on that account are termed heteroecious, there is frequently more than one method of propagation. Protozoan forms which come under this category are said to multiply by schizogony, a kind of multiple fission, and by sporogony, a process of spore-formation preceded by conjugation. Sporogony usually either makes possible the invasion of a new host or takes place only in connection with the second or intermediate host. The evident food relations between the hosts of many of the heteroecious animal parasites, such as the mosquito and man and various mammals in the case of malarial forms, renders the association of the unlike hosts not so difficult to appreciate.

In the higher fungi, especially in the group popularly known as the rusts (Uredinales), there are many instances of heteroecious parasitism and in none of them is there the slightest hint of a relationship between the two hosts. There are many forms inhabiting coniferous trees and from these they may pass over in their alternate stage to plants widely separated in taxonomic classification. Thus we may find a form alternating between a fir and a fern, a cedar and an apple, or a pine and a composite. It seems impossible to escape the conviction that some extraordinary relationship must exist between these two sets of hosts occupied by a heteroecious form and yet in the half-century since we have had definite proof of heteroecism in the rusts no satisfactory explanation has been forthcoming. In North America we have today almost exactly one hundred demonstrated cases of heteroecious life-cycles in this group. The rusts are of especial interest from our present point of view not only because of heteroecism but also because of the existence of autoecism within the same group, and the consequent opportunity to compare these two types of adaptation. Heteroecious forms always possess what may be termed a long life-cycle divided necessarily into two phases, on the one host consisting of telia, either alone or accompanied by uredinia, and on the other host of aecia, preceded by pycnia. Telia, uredinia, and aecia produce spores usually unlike one another and are all for purposes of propagation. Pycnia produce simple spores unlike any of the others and of unknown function. Autoecious forms may exhibit the same number of spore-forms and in the same sequence as just described for heteroecious forms, or they may have the aecia and uredinia lacking. In this case the pycnia, when present, are followed at once by telia and we have what may well be designated as a short life-cycle. The heteroecious forms always show well developed pleomorphy whereas the autoecious forms may or may not. The presence or absence of urediniospores, which simply repeat themselves over and over, is held to be of no fundamental importance in the formation of a life-cycle. It is understood that telia are always present and that pycnia usually (but not always) follow from telial infection. If a heteromorphic spore-stage (aecia) follows the pycnia the form is thrown into the long-cycle series without regard to the presence or absence of a second heteromorphic stage (uredinia).

Ever since heteroecism has been definitely known to exist in this group, or for fifty years, naturally there have been speculations concerning its origination. Within the last ten years since sexuality and an alternation of generations have been demonstrated the character of the speculations has been somewhat modified. The probable evolutionary tendencies within such a remarkable group of obligate parasites must have an important bearing upon our general conception of the genetic physiology of parasitism.

If we accept a view, which has found much favor, that the complex heteroecious types have been derived by amplification from the simple, autoecious, short-cycle forms, we then find it necessary to explain how parasites, in which degeneration might be expected, have made unprecedented advances. To be sure it seems most logical to derive the complex from the simple and the amplification, since it is in the sporophytic stage, is in accord with the conditions found in independent plants. But the questions immediately arise whether we can expect such obligate parasites to parallel the development of higher plants and whether we need to make such assumptions in order to explain present conditions. In the light of our observations on the behavior of parasites it seems that we ask a good deal of both evidence and probability in seeking to align these parasites with the independent higher plants on the basis of the development of the alternating generations.

Both short- and long-cycle forms agree in the gametophytic generation which is initiated by the reducing germination of the teliospore and ended by a doubling conjugation previous to the production of the first spore-structure (the pycnia being disregarded). In the short-cycle condition the first spore-structure is another telial stage hence the sporophyte is represented only by the teliospores themselves and a small amount of growth accessory to their production. In the long-cycle condition the first spore-structure following the conjugation may be known as the aecial stage without regard to its form or structure. In all cases the aeciospores give rise to a plant body (mycelium) which is sporophytic. In some forms it produces repeating spores, either like or unlike the aeciospores, but ultimately forms the telial stage, the end of the sporophytic phase. In heteroecious forms the two phases are produced upon the unlike hosts. Reasoning by analogy we are justified in regarding the gametophyte as the primitive generation and it would seem to follow that the forms with the least developed sporophyte should be nearest the ancestral conditions. By a progressive development of the sporophyte, a prolongation of the double nucleated phase, we have an evolution which is comparable with the course of development of the higher plants. Some investigators have become so confident that this is a reasonable presumption that they have ceased to argue this phase of the problem but have gone on to discuss the origin of heteroecism, how the jump from autoecism to a new host could have come about, and which was the original gametophytic host and which the secondary one.

If the rusts have made such advances in their sporophytic generation we have a condition which may force us to modify our ideas of parasitism. The whole question is inseparably connected with the large problem of the genetic relationship of parasites. The question whether this group with all its complexity conforms to the nature and development of other parasites or stands as an exception is one which interests us today.

Those who have regarded the rusts, in spite of their complexity, as a degenerate group of parasites also have advanced theories as to the probable course of development. It may be idle to speculate further with such theories but perhaps another viewpoint may permit new relations to be perceived. According to one view pleomorphy and even heteroecism are held to be the primitive condition and the autoecious short-cycle forms are regarded as the latest in evolution having arisen by a process of degeneration and reduction. It is not denied that there must have been amplification some time in order to attain the long-cycle condition but it is believed that this did not take place after those organisms became parasites. Undoubtedly the long-cycle forms represent the highest development but probably not the latest. As suggested in a foregoing paragraph there is much in favor of the parasitic fungi having passed through an intermediate saprophytic stage. Ultimately, of course, they must have come from independent ancestors. The existence of independent thallophytes and saprophytes showing well developed pleomorphy indicates that this feature is not one which can be considered as having any peculiar connection with the parasitic mode of life. The transition of complex pleomorphic forms into heteroecious parasites may not seem an easy step but is not more difficult to appreciate than the interpolation of one or two new stages, upon an entirely foreign host, into the life-cycle of a simple parasite.

Since our present interpretation of the evolution of the higher plants is the rise of the sporophyte and the decline of the gametophyte much has been made of an analogical application to these parasites. It has been pointed out that those forms with the longest sporophytic stages must have arisen in a progressive way. While this is doubtless the case there is much doubt whether they have progressed as parasites and whether the present short-cycle forms can be looked upon as representing their ancestors. It should be pointed out that there has been no decline of the gametophyte unless it be in the loss of pycnia in some species. However, the only forms in which pycnia are known to be absent are short-cycle forms, which are according to the theory of ancestral nature. The pycnia are without doubt functionless today. It would be odd indeed if the gametophyte of the latest type in evolutionary history should always develop a useless structure not universally known in its ancestral forms. Surely this is not in conformity with the higher plants. There has been much discussion over the interpretation of the pycnia in the rusts. The view that they represent vestigial male organs is highly plausible. Without much doubt they have not been functional since the parasitic adaptation. A former sexuality in which an Aecidium-like structure bore the female organs is now replaced by a somatic doubling conjugation in the mycelial mass below the spore-structure. The eventual disappearance of the pycnial stage might be anticipated in the latest forms. If this has any bearing it points toward the short-cycle autoecious type as the most recent for here the pycnia may be omitted although in ontogeny there elapses a time for their development.

In a parasitic group where there is such a close relation between parasite and host we might gain some idea of genetic relationship from a study of the distribution of the different types of rusts upon the series of hosts. Although the phylogeny of the hosts may not be regarded as settled the arrangement will permit this sort of a general comparison. It seems logical to assume that the lowest hosts would be parasitized by the more primitive forms while the higher host orders would be expected to have upon them the more advanced types. As already indicated we recognize but three types of parasites, heteroecious long-cycle, autoecious long-cycle, and autoecious short-cycle. The ferns are the lowest hosts for these parasites and their forms are pleomorphic and heteroecious. In order to have some numbers available a careful survey of North American forms having a definite known life-cycle has been made. Out of fifty species on Coniferales forty-seven are heteroecious. Glumaceous rusts are heteroecious with a single possible exception. In the Lily order while only seven are heteroecious, twenty-three are autoecious long-cycle forms, with a single short-cycle form. The Ranales have the three types almost equally distributed. In the large rose order the long-cycle forms greatly predominate but autoecism is three times more prevalent than heteroecism. Upon the final great alliance, Campanulales, we find heteroecious phases but so far as present known life-cycles are concerned they are only half as numerous as short-cycle forms, the figures being thirty-two and sixty. If we make comparisons within the short-cycle series we find that they are almost unknown upon the lower orders whereas sixty out of a total of one hundred forty-eight known forms are found upon the highest order. If this sort of evidence is competent its indication is certainly plain.

In a recent paper Olive has taken it for granted that autoecism is the original condition and has brought forward arguments bearing on the question as to which of the heteroecious hosts is the primary one. With his premises as a basis he comes to the very logical conclusion that the present aecial host was the original host of the hypothetical autoecious ancestor. Part of the argument is that the gametophytic generation being the more primitive should be on the primary host. To evolve the heteroecious condition the gametophyte has remained unchanged but the sexual fusions have furnished the invigorating influences which are responsible for pleomorphy and the pleophagic habit. It cannot be denied that sexual fusions should furnish invigoration but those fusions found here which appear to be a degenerate substitution for a former fertilization do not seem adequate to account for such a profound change in the life of a parasite.

If we are to take the view that the present aecial host is the original and primary one, then it would seem reasonable to expect the aecial stages to be on the more primitive hosts as a rule. The condition found in our North American heteroecious forms does not bear out this expectation for we find out of ninety-nine species that seventy-eight have aecial hosts standing higher in classification than their telial hosts. To support the argument that the gametophytic host was the original autoecious one, it has been urged that there are instances where short-cycle forms are known on the aecial hosts of heteroecious species, the teliospores of the two showing structural parallelisms so striking that some kind of relationship is strongly suggested. *Puccinia mesnieriana* a short-cycle form occurring on *Rhamnus* and having teliospores peculiarly like *Puccinia coronata*, a heteroecious grass form having its gametophytic stage on *Rhamnus*, has been cited. There are numerous other cases. *Puccinia Xanthii* is an autoecious form on *Xanthium*, which harbors the aecial stage of a sedge rust, *Puccinia Cyperi*. *Polythelis fusca*, a short-cycle form on *Anemone*, has teliospores identical with *Tranzschelia punctata* which has its telia on *Prunus* and its aecia on *Anemone*. Numerous other cases could be mentioned. May the evident genetic relationship best be explained by amplification or reduction? Not only does the latter more nearly conform to the physiology of parasitism but also agrees with certain conceptions of differentiation which have been formed from experimental genetics. Based upon many considerations we find Bateson saying that he feels no reasonable doubt that we may have to forego a claim to variations by addition of factors, yet variation by loss and fractionation of factors is a genuine phenomenon of contemporary nature. If there is a possibility that we may have to dispense with additions from without in independent forms how much more strongly does such a situation press its claim for recognition in parasites. To return briefly to the associated long- and short-cycle forms above mentioned we find that no startling variation has to be assumed in order to derive the latter from the former. If on the gametophytic host, following the sexual fusion, there should be produced at once teliospores instead of an intercalation of one or more polymorphic spore-stages, the proper conditions for a short-cycle autoecious form would be at once established. In heteroecious forms only the reduced basidiospores following teliospore germination can infect the aecial host. In the abbreviated condition just outlined we have the necessary requirements for reinfection and maintenance of a short-cycle telial form on what was the original aecial host. Believing that the only fundamental stages are those of sexual fusion and teliospore formation neither is disturbed by such a shortening process. Teliospore formation which was an inherent capacity simply takes place sooner than formerly without the intervention of a somatic stage of such extent between sexual fusion and reduction. If teliospore production is to take the place of the former aeciospore formation there might be two expectations concerning their nature. They might be exactly like the former teliospores in which case nothing happens except the pulling of the stage backward to the other host, or they might be expected to have the morphology of the aecidiospores but behave physiologically like teliospores. The so-called genus *Endophyllum* fits the latter hypothesis and may have arisen in some such manner. The cases cited and numerous others fit the former. Such a theory does not fit badly with the present distribution of the types of rusts upon the phylogenetic series of host plants. Recalling the fact that the tendency for heteroecious species is to have the gametophytic hosts higher in classification than the telial hosts we must expect the short-cycle forms which are to occupy the former gametophytic hosts to show an upward movement which would result in their occupation of the higher orders. I have already shown that is in accord with the facts based upon a survey of North American forms. Although it may be objected that these considerations do not explain the real origin of the group it may be claimed that they do express a trend of evolution, since a time when the group attained a parasitic mode of life, which accords with the course of development everywhere bound up with parasitic adaptations.

Someone has said that nature produces individuals while man has created species. This seems hardly a proper observation for higher plants and animals but it applies well to the lower parasites. The fact that we hear of "physiological" species, "biologic" races, and "formae specialis," in parasites is but an admission that man is the inventor of "species" of some groups and in order not to be misinterpreted finds it necessary to qualify the term. Cook and Swingle have pointed out that "normal and long-sustained evolutionary progress is not accomplished on single or narrow lines of descent, but is possible only for large companies of interbreeding individuals; that is to say, for species." Certainly in all organisms where we have interbreeding and interweaving of distinct lines of descent there is such a thing as a real specific group but in the parasitic fungi all traces of the coherence of such a group has been lost. With the exception of the mucors, where the interweaving of strains is definitely known, and the possible occurrence of sexual strains in some downy mildews and anthracnoses, there is no suggestion of groups of interbreeding individuals. The individuals continue their existence without relation to other individuals. It is clear that man makes the species here solely for his convenience and he must decide whether he will make morphology or physiology his standard. If it is true that progress cannot be maintained along narrow lines of descent this will assist in understanding why advances are not to be found in the parasitic fungi for here the lines are the narrowest possible, simply the continuations of individual existences. If we are given an individual spore we can start a life-cycle which will bring us back to more spores of the same sort and we may raise generation after generation but they are descendants of a pure line in no way influenced by individuals of different origins. The factors which may influence them are their hosts and the environment.

Through morphology we form our judgment concerning the possible similar origin of individuals which come to us to classify. In the parasitic fungi as a rule it is only the reproductive features that receive morphological consideration. If we considered only dead specimens there would be no difficulty, but with the advent of experimental culture work, perplexing questions have arisen. The work of Eriksson, Klebahn, and others served to emphasize this matter but it is clear from DeBary's writings that he was aware of the specialization of a parasite to a host although he did not use the form of expression now prevalent. Morphological equivalents growing upon the closely allied hosts may not have the same behavior. The powdery mildews, anthracnoses and rusts furnish many familiar instances. This means that the plant body is coming in for attention and that the consideration must be of a physiological nature. The question whether forms structurally alike but reacting physiologically differently should be regarded as belonging to the same species or a race, etc., may be an interesting one but is not the most important one. The bacteria are notable organisms which raise such questions. But the genetic relationship is of greater significance. It is a common view that the forms morphologically alike must have had a common origin and that physiologically specialized forms have resulted by progressive variability on a special host. Nutritional adjustment and other interacting factors have been suggested as associated with the variations but no demonstration up to the present has made the matter at all clear. It has been assumed that continual specialization will lead eventually to structural differentiations. There seems to be nothing in the methods of descent which would prevent the carrying forward of any variation once established. It is rather a question of how the physiological relations between host and parasite or the environment might operate to bring about a diversity of form and structure.

Very little is known of the possible effect of the ordinary factors of environment upon the development of a parasite. There is some evidence regarding effects upon distribution. After a detailed comparison of the geographical distribution of hosts and parasites in one group of fungi, the writer came to the conclusion that the environment had little if any influence at all, but such apparently is not true for all kinds of parasites. Ward has shown that external influences may undoubtedly exert important effects. Too high a temperature during incubation, starving the host of carbon dioxide or salts, or heating or cooling the roots may ruin a fungus and stop infection. Salmon has also carried out investigations to show that external as well as internal features are concerned in determining whether parasites may attack and continue development.

As a conclusion we may consider, with brevity, parasites as an aid in determining genetic relationships in their hosts. Cobb has written on this subject in a very enthusiastic way, pointing out that parasites may be used (1) as an aid in discovering specific and generic relationships, (2) in following metamorphoses, (3) in physiology, (4) in chemistry. I am particularly interested in the first of these. I trust I may be pardoned for drawing my examples from a group in which I have long had a special interest. A recently published result brings this phase of the subject to mind. The members of the genus *Gymnosporangium* were long supposed to alternate solely between the juniper and apple families. Upon the morphology of a spore-form found upon a member of the rose family I suspected its connection to a cedar rust and assisted in proving the relationship. Later a similar case was discovered in the hydrangea family and it, too, was established. The Malaceae, Rosaceae, and Hydrangeaceae have always been regarded as close relatives, being included in the order Rosales. Recently Fromme has reported a fourth family, Myricaceae, as furnishing a host for a *Gymnosporangium*. Since the other three families are evidently related, there is a strong suggestion that this one should stand nearby in the scale of classification. In Engler and Prantl's system it is, however, in the fourth order of the Dicotyledoneae while the Rosales is the twenty-first order. The Myricales order has a similar low position in the latest manuals of Gray and Britton. It is interesting to note that Bessey, on the other hand, places the family Myricaceae in the order Sapindales which he derives from the Rosales through the Celastrales. The latter arrangement is much more strongly supported by the parasites than the former. In this same group of fungi there is some evidence regarding the relationship of the other series of hosts. It is generally accepted that the § *Oxycedrus*, of the genus *Juniperus*, with its subulate leaves, is of earlier origin and probably ancestral to the § *Sabina*, which has its leaves subulate when young but scale-like when mature. The species of the § *Oxycedrus* are distributed in both hemispheres and appear to be identical. Species of the § *Sabina* are widely distributed but certain species are indigenous to one hemisphere and certain ones to the other, there is not one that is common to both. The parasites of the genus *Gymnosporangium* parallel the condition of the hosts exactly. We do not find the same species indigenous to both hemispheres on the § *Sabina* but we do on the commonly distributed section. The distribution of the hosts would suggest separate origins of the derived section in North America and the Old World and this theory is strongly supported by the condition of the parasites. These examples will suffice to illustrate the matter. Our knowledge is too incomplete to determine the real value of this phase of the subject and yet we may conclude that a knowledge of the parasites is worthy of consideration in a study of the hosts.

PENNSYLVANIA STATE COLLEGE,
STATE COLLEGE, PA.